How do subordinate and dominant species in semi-natural grasslands relate to productivity and land-use change?

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How do subordinate and dominant species in semi-natural mountain grasslands relate to productivity and land-use change?

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Running tittle: Abandonment of pasturing reduces subordinate species

Abstract

Changes in agricultural practices of semi-natural mountain grasslands are expected to modify plant community structure and shift dominance patterns. Using vegetation surveys of 11 sites in semi-natural grasslands of the Swiss Jura and Swiss and French Alps, we determined the relative contribution of dominant, subordinate and transient plant species in grazed and abandoned communities and observed their changes along a gradient of productivity and in response to abandonment of pasturing.

The results confirm the humpbacked diversity-productivity relationship in semi-natural grassland, which is due to the increase of subordinate species number at intermediate productivity levels. Grazed communities, at the lower or higher end of the species diversity gradient, suffered higher species loss after grazing abandonment. Species loss after abandonment of pasturing was mainly due to a higher reduction in the number of subordinate species, as a consequence of the increasing proportion of dominant species.

When plant biodiversity maintenance is the aim, our results have direct implications for the way grasslands should be managed. Indeed, while intensification and abandonment have been accelerated since few decades, our findings in this multi-site analysis confirm the importance of maintaining intermediate levels of pasturing to preserve biodiversity.

Zusammenfassung

Änderungen in der Bewirtschaftung naturnaher Bergwiesen können die Struktur von Pflanzengesellschaften und deren Dominanzmuster verändern. Anhand von Vegetationsaufnahmen 11 naturnaher Wiesen des Schweizer Juras und der Schweizer und Französischen Alpen erfassten wir den Anteil der dominanten, untergeordneten und transienten Pflanzenarten in beweideten und aufgelassenen Pflanzengemeinschaften, beobachteten ihre Veränderungen entlang eines Produktivitätsgradienten und ihre Antwort auf die Aufgabe der Beweidung.

Die Ergebnisse bestätigen den glockenförmigen Zusammenhang zwischen Artenreichtum und Produktivität in naturnahem Grünland, insbesondere aufgrund der Zunahme von untergeordneten Arten bei mittlerer Produktivität. Beweidete Pflanzengesellschaften am unteren oder oberen Ende des Pflanzenvielfalts-Gradienten verloren nach Aufgabe der Beweidung mehr Arten. Der Artenverlust nach der Beweidungsaufgabe war vor allem ein Resultat der höheren Reduktion von untergeordneten Arten als Folge des steigenden Anteils hochwachsender Arten.

Unsere Ergebnisse haben direkte Auswirkungen auf die Art und Weise, wie Grünland bewirtschaftet werden sollte. Während die Intensivierung und die Aufgabe beweideter Flächen seit Jahrzehnten schneller vorangehen, bestätigen die Ergebnisse dieser Multi-Site-Analyse die Bedeutung einer mittleren Beweidungsintensität für den Erhalt der Artenvielfalt.

Keywords: diversity-productivity relationship, grazing, land-use management, plant community structure, species coexistence.

Introduction

Semi-natural mountain grasslands are widespread components of north-temperate landscapes and play an important role by providing fodder for livestock and acting as reservoirs for both carbon (Follett & Reed 2010) and biodiversity (Mariotte et al. 2013a). These ecosystems host species-rich communities with up to 40 plant species per square meter but are among the most endangered ecosystems in Europe, threatened by both land-use (Silva et al. 2008, Fava et al. 2010) and climate change (Jentsch et al. 2009; Mariotte et al. 2013b). Indeed, changes in agricultural practices, which have been accelerated since the 1950 in Central Europe are leading to either agricultural intensification or abandonment (Gillet & Galandat 1996, Buttler et al. 2012). While plant community structure (species diversity and composition) is largely the result of management (regular grazing) of semi-natural grasslands, land-use changes are likely to modify this structure and, as a consequence, perturb community stability and ecosystem functioning. Therefore, it seems essential to understand which structural components of plant communities contribute most to species diversity and how they are affected by land-use changes.

The easiest way to classify components of floristic biodiversity is to order species according to their relative abundance and to define their functional role (Grime 1998). This approach was further developed by using dominance-diversity profiles, which allowed to distinguish three components: dominant, subordinate and transient species (Grime 1987, 1998). Those elements may vary in species richness, functional traits and functional groups. According to Grime, dominant species are few in number, tall and more expansive in morphology and produce high quantities of biomass. Therefore, immediate influence of plant communities on the ecosystem properties is expected to be primarily determined by traits of dominant species (“mass ratio theory”, Grime 1998). Subordinate species are generally more numerous, but smaller in stature and form a low proportion of the total community biomass.

By contrast, transient species, which generally do not persist after years and appear only briefly as seedlings, may replace the other species or colonize new areas after disturbance (“founder effects”).

Species-rich ecosystems, such as semi-natural grasslands, are driven by coexisting species in a strict dominance hierarchy where superior competitors (dominants) can displace inferior competitors (subordinates) from occupied patches whereas inferior competitors cannot displace superior competitors (Amarasekare 2003). Subordinate species have no access to patches occupied by dominants, but their better resource efficiency (“filter effects”, Grime 1998) allows them to establish in patches that dominants are not able to colonize. This mechanism leads towards spatial niche differentiation between the two species-groups and resource complementarity instead of resource competition. Species coexistence, through niche partitioning, is mainly the result of differences in light availability, soil fertility and disturbance which all contribute to ecosystem productivity. Productivity has been demonstrated to be a function of species diversity in artificially created grasslands (Hooper et al. 2005) but a meta-analysis suggested that, in natural grasslands, diversity is a function of productivity (Grace et al. 2007). Diversity-productivity relationships of species-rich communities follow in general a humpback model (Grime 1973) where species diversity is higher at intermediate levels of productivity, fertility and disturbance (Odum 1963, Hughes et al. 2007). However, the humpbacked pattern has generated strong debate in ecology and recent meta-analytical syntheses concluded that various patterns can occur (Gillman & Wright 2006). Indeed, based on standardized samples from 48 herb-dominated plant communities on five continents, the productivity-diversity relationship shows different patterns depending on land-use history and management of the sites (Adler et al. 2011). Nevertheless, evidence of a humpback relationship was found when including restored prairies, pastures and old fields in the analysis (Adler et al. 2011), confirming findings of Grime (1973) for species-rich communities. According to the theory, productive grasslands with high soil fertility and/or light availability are sites of competitive exclusion, which allows dominance of some species, while low productive grasslands with low soil fertility and/or light availability are stressful environments for plant species (Al-Mufti et al. 1977). Therefore, higher species richness should be observed at intermediate productivity levels, which represent the equilibrium between disturbance and dominance. Concerning the role of subordinate species it is further suggested (Grime 1987) that subordinate species represent a higher proportion of species within the hump of the diversity-productivity model but this statement has not been confirmed by field experiments and calls for verification.

In semi-natural mountain grasslands, grazing by large herbivores is an important driver for creating and maintaining biodiversity and many studies showed that species diversity decreases after abandonment of pasturing (Kohler et al. 2006a,b, Sebastià et al. 2008, Marion et al. 2010, Parolo et al. 2011). In these ecosystems, the persistence of subordinate species seems to be closely related to the activity of large herbivores, which reduce competition from dominant species through gap creation (Mariotte et al. 2012a, Kohler et al. 2006b) or grazing (Tahmasebi Kohyani et al. 2009, Gillet et al. 2010). Inversely, the exclusion of cattle can lead to the dominance of competitive tall-growing species (Tasser & Tappeiner 2002, Mayer et al. 2009), which reduces light availability for small-stature ground layer species. These findings confirm the hypothesis that intermediate disturbance through cattle activity may over-proportionally benefit small-stature subordinate species while cattle abandonment is expected to reduce the abundance of these species.

In this multi-site study, we aim at describing the structure of plant communities in semi-natural mountain grasslands along a productivity gradient. The study includes eleven sites of the Swiss Jura and the Swiss and European Alps, which differ in their aboveground biomass production. The abundance of dominant, subordinate and transient species (species-groups) is determined and related to species diversity. We then compare the abundance of these species-groups in paired grazed and abandoned plots from nine sites to test whether the abundance of subordinate species decreases after abandonment and how this impacts plant species diversity.

Materials and methods

Study sites

In order to have a large productivity gradient, we brought together results of eleven similar studies carried out in semi-natural grasslands of the Jura and the Alps (Kohler et al. 2006a,b, Spiegelberger et al. 2006, Vandenberghe et al. 2008, Gilgen & Buchmann 2009, Mariotte et al. 2013a, see Appendix A: Table 1). The sites, situated between the montane and the subalpine belt, were floristically similar and dominated by *Festuca nigrescens, Agrostis capillaris, Dactylis glomerata, Trifolium repens* and *Taraxacum officinale*. The eleven sites were extensively grazed by cattle (summer grazing, see Appendix A: Table 1) and nine of them included also 3- to 5-years-old abandoned plots. Grazed and abandoned communities were situated either in the same place (sites 1, 4, 6, 7 & 10) or with a maximum of 5 km between them but in similar conditions of exposition and inclination (sites 2, 5, 8 & 9, see Spiegelberger et al. (2006) for a more detailed description). Each site included five very homogeneous plots except for sites 1, 4 and 6 where three plots were available. Aboveground community biomass production was measured at peak biomass by harvesting standing crop above 5-7 cm in each plot, drying at 60 °C for 72 hours and weighing. Vegetation surveys were done in mid-summer using different methods: Braun-Blanquet index (site 3), biomass sorting (sites 7, 10 & 11), point quadrats (sites 1, 4 & 6) or estimated to the nearest per cent (sites 2, 5, 8 & 9). The sampled surface corresponded to 1 m^2, except in site 11 where it was 0.2 m^2. Smaller quadrats were justified here because no further species were expected to be included by a 1 m^2 sample, and the species number was used without correcting for quadrat size. Proportion of species assessed in the field as Braun-Blanquet index, cover or biomass was transformed in relative proportion (%) to allow comparison between sites.

Plant community structure (analysis A)

For each site, species diversity was calculated as the mean species number in grazed plots (n = 3 or 5). We averaged relative species proportion observed in replicated plots (n = 3 or 5) to obtain the mean relative species proportion per site. Species were classified in competitive hierarchical groups (Grime 1998, Mariotte et al. 2013a,b) for each site according to a frequency-proportion curve (see Appendix A. Figure 1) based on species frequency and cumulative proportion. Species were ranked by proportion in ascending order and cumulated to obtain cumulative proportion value for each species. 100% frequency means that the species is present in all plots and 100% cumulative proportion corresponds to the most abundant species. A species was classified as dominant if its frequency was greater than 50% and its cumulative relative proportion greater than 12%. A species was classified as subordinate if its frequency was greater than 50% and its cumulative relative proportion between 2 and 12% (adapted from Grime 1998). The other species were classified as transient plants. Vegetation surveys were done during several years (except in sites 2, 5, 8 & 9) and we confirmed that our species-groups selection was consistent over these years. Moreover, further analysis on plant functional traits in sites 7 and 10 showed that selected species-groups differed (Mariotte et al. 2013a), with dominant species linked to high specific leaf area (SLA) and plant height whereas subordinate species are associated to low SLA and small-stature traits. We determined the relative contribution (%) of the three species-groups to the diversity along a productivity gradient containing the 11 sites. The relative contributions of dominant, subordinate and transient species correspond to the number of species per species-group divided by the total number of species in the respective plot.

Abandonment of pasturing (analysis B)

In a second analysis, we analysed the effect of cattle abandonment on the structure of plant communities and put this in relation to changes in species diversity. Species diversity was calculated as the mean species number in abandoned plots (n = 3 or 5) and compared with the productivity of abandoned communities and with the species diversity of nearby grazed communities at the same location. As previously, dominant, subordinate and transient species were determined in abandoned communities and changes in the relative contribution of the three species-groups (plant community structure) in abandoned plots were plotted against the diversity in grazed communities. For each site, proportional changes in dominant species (subordinate or transient) were calculated as the difference in log between the number of dominant species (respectively subordinate or transient) in abandoned plots and in grazed plots. The use of log allows to account for the effect of initial species diversity and highlights the negative, neutral or positive effects of abandonment. In addition, to test whether abandonment of pasturing benefits tall-growing species at the expense of small-stature species, we classified all species from vegetation surveys in one of those two groups and calculated their relative proportion in grazed and abandoned communities. Species growing taller than 15-20 cm were classified as tall-growing species while the others were classified as small-stature species. Data on canopy height was taken from "Flora Helvetica" (Lauber & Wagner 2007) and the "LEDA trait database" (Kleyer et al. 2008).

Statistical analysis

In the analysis (A), we first focused on the relationship between species diversity and productivity and then on the relative importance of species-groups in this relationship. Species diversity, productivity and abundance of species-groups were summarized into mean values per site. In the second analysis (B), we explored the relationship between the species diversity in abandoned and grazed communities and observed the effect of abandonment on species-groups contribution at 9 sites (see Appendix A: Table 1). Polynomial models (degree 2) were calculated with the orthogonal polynomial function (poly {stats}) in R version 2.14.1 (R Development Core Team, 2011). Statistical significance of models (p-value) and multiple R^2 values were obtained using ANOVAs to estimate the goodness-of-fit. The differences in the relative contribution of tall-growing versus small-stature species between grazed and abandoned communities were analysed using linear mixed-effects models specifying plot (n = 3 or 5) nested into site (n = 9) as random factors.

Results

Diversity-productivity relationship in grazed plots

The mean species diversity per site ranged from 13.2 ± 0.6 species to 36.8 ± 1.1 species along the productivity gradient, which ranged from 99 ± 7 to 590 ± 77 g dwt.m^{-2}. Species diversity was clearly linked to productivity (Fig. 1A) and best explained by a polynomial function ($F_{2,8}$ = 11.525, P < 0.01, R^2 = 0.75). Dominant species represented between 41 and 61% of species but their contribution to the total diversity remained similar along the productivity gradient (Fig. 1B). By contrast, subordinate species, representing 15 to 36% of species (Fig. 1C), followed a polynomial distribution along the productivity gradient ($F_{2,8}$ = 10.065, P < 0.01, R^2 = 0.72). The contribution of subordinate species to total species diversity was less important at low and high productive sites but higher at intermediate productivity. The transient species, which contributed from 9 to 41% (Fig. 1D), followed an inverse pattern, fitted by a significant polynomial function ($F_{2,8}$ = 6.671, P < 0.05, R^2 = 0.63). Soil dissolved inorganic nitrogen, which had been measured in four sites (see Appendix A: Table 1), was positively correlated to productivity ($F_{1,2}$ = 119.792, P < 0.01, R^2 = 0.98).

Abandonment of pasturing

In abandoned plots, productivity did not affect species diversity (see Appendix A: Figure 2; Polynomial: $F_{2,6}$ = 0.332, P = 0.73, R^2 = 0.09; Linear: $F_{1,7}$ = 0.766, P = 0.41, R^2 = 0.10).

However, species diversity of abandoned communities was linked to the species diversity of paired grazed communities (Fig. 2A), which was assumed to represent the initial species diversity before pasturing of the sites was abandoned. Mean species diversity in abandoned plots was either similar or lower compared to mean species diversity in grazed plots (Fig. 2A). The loss of species due to abandonment was remarkably pronounced in initially low (e.g. 10 species less in abandoned site 9 compared to the grazed site 9) and highly diverse sites (e.g. 24 species less in site 5) resulting in a significant polynomial relationship between initial species diversity and current diversity ($F_{2,6}$ = 62.606, $P < 0.001$, R^2 = 0.95).

At the species-group level, the differences in number of dominant ($F_{2,6}$ = 12.616, $P < 0.01$, R^2 = 0.81) and subordinate species ($F_{2,6}$ = 11.501, $P < 0.01$, R^2 = 0.79) showed the similar polynomial pattern as observed for species diversity whereas the difference in number of transient species (Fig. 2D) was similar in grazed and abandoned communities (-12% to +19%). The difference in number of dominant species (Fig. 2B) was similar in four sites, higher in one site (+14%) and lower in four sites (respectively -58% and -45% in lower and higher initial species diversity). In abandoned communities, the difference in number of subordinates (Fig. 2C) was high in eight of the nine plots (-6% to -94%) and much higher than the difference in number of dominants, especially in sites with high species diversity. The analysis of vegetation surveys showed that the identity of dominant species was almost similar in grazed and abandoned communities, while the identity of subordinate and transient species showed more variation between both communities. Indeed, some transient species observed in grazed plots became subordinates in abandoned plots and vice versa.

The relative contribution of tall-growing species was significantly higher ($F_{1,38}$ = 31.788, $P < 0.001$) in abandoned plant communities (81%) compared to grazed communities (63%) at the expense of small-stature species.

Discussion

Plant community structure and the diversity-productivity relationship

This multi-sites analysis, including 11 semi-natural mountain grasslands, determined plant community structure along a productivity gradient. In analysis A, we highlighted a diversity-productivity relationship, which was best fit by a polynomial model. These results confirm the diversity-productivity dependency suggested by various authors (Al-Mufti et al. 1977, Grime 1973, Grace et al. 2007, Adler et al. 2011). In pastures, plant communities are continuously disturbed by cattle activities (Gillet et al. 2010, Kohler et al. 2006a,b), and disturbance due to grazing was constant and similar for the eleven sites (see Appendix A: Table 1). Here, we suggest that the productivity gradient is more related to soil fertility as concentrations of dissolved inorganic nitrogen in soil increase along this gradient. In our study, the maximum diversity (30-35 species) occured at intermediate productivity (between 180 and 420 g dwt.m^{-2}) and supports the humpback model of Grime (1973, 1987), where species diversity is predicted to be higher at intermediate productivity and fertility (Odum 1963). Our findings therefore confirm that intermediate productivity favours species coexistence in semi-natural grasslands.

Interestingly, the contribution of species-groups differed along the diversity-productivity relationship. Grime (1987) proposed that low productivity favours transient species, intermediate productivity favours subordinate species and high productivity favours dominant species. Indeed, in our analysis, the proportion of subordinates peaked at intermediate productive sites and we confirm that intermediate productivity favours the presence of subordinate species through coexistence, and thus increases species diversity. In contrast to Grime’s hypothesis (1987), the proportion of transient species increased in our multi-sites study at low and high productivity sites, whereas dominant species did not change along the productivity gradient, representing about 50% of the species diversity. In contrast with Grime's work, which included a wide range of herbaceous vegetation, we based our analysis only on semi-natural mountain grasslands. In these ecosystems, cattle activities such as grazing and trampling, even at low intensity, tend to prevent potentially competitive species from attaining maximum size at high productive sites (Grime 1973, Augustine & McNaughton 1998). Therefore, we suggest that large herbivores may stabilize the proportion of dominant species along the productivity gradient, whereas subordinate species prevent low competitive transient species to appear at intermediate productivity.

Abandonment of pasturing in semi-natural grasslands

In the second analysis (B), we showed that, in 7 out of 9 cases, species diversity was lower in abandoned communities compared to grazed communities which confirms previous observations in species-rich pastures (Sebastià et al. 2008, Marion et al. 2010, Parolo et al. 2011). Interestingly, the difference of species diversity associated with land abandonment was a function of the initial species diversity of the site (species diversity when plots were still grazed) with high and low diverse sites being more affected by abandonment. Plant productivity differed in abandoned communities but we did not find a clear relationship between the loss of species diversity and/or the differences in plant community structure.

Plant community structure differed in abandoned plots, with a loss of species diversity, and these differences can be interpreted here as a function of initial species diversity (e.g. diversity of the grazed plots). The loss of subordinate species was higher than the loss of dominants, showing that abandonment of pasturing over-proportionally affects subordinates. The mechanisms underlying this pattern are difficult to explain as various components of cattle activity, such as grazing, trampling and dunging, may influence plant community (Kohler et al. 2006b). Selective grazing is especially high at low cattle density (Klapp 1971) as was the case in the sites included in our study. Selective grazing is expected to increase species diversity when dominant species are grazed (reduction of dominance), and to decrease species diversity when subordinates are grazed (increase of dominance). In our study, species diversity was lower in the absence of grazing (abandoned plots), suggesting that selective herbivory on dominants occurred in grazed communities. A major response to grazing is the promotion of ground-layer species due to the vertical defoliation (Dupré & Diekmann 2001). This adaptation favours small subordinate species, which are expected to be less affected, whereas dominant plants, which are often characterised by higher nutrient requirements and growth rate, are vulnerable to foliage losses (Augustine & McNaughton 1998). Subordinate species have shown to regrow better after grazing than dominants due to their physiological plasticity or because they benefit from reduced competition from grazed dominants (Tahmasebi Kohyani et al. 2009, Mariotte et al. 2012a,b). However, although grazing significantly favours subordinate species, increasing nutrient levels may counteract the negative effect of grazing on dominant species (Tahmasebi Kohyani et al. 2009). Indeed, the fertilizing effect of dung favours competitive dominants (nutrient demanding tall species) at the expense of stress-tolerant or perturbation-resistant subordinates (Gillet et al. 2010). Trampling by cattle must also be considered as it provides spatial heterogeneity (gaps), which may benefit subordinate species (Kohler et al. 2006b, Mariotte et al. 2012a). Moreover, while the number of dominant species was lower, our observations on canopy height showed that the proportion of tall-growing species was higher in abandoned plots at the expense of small-stature species (less light availability or nutrient resources), which confirms that dominance increased after abandonment of pasturing. Therefore, we suggest that the higher loss of subordinate species may be due to the absence of both grazing and trampling but also to the increase of dominance, which impedes their development, while dominant species are only reduced by the absence of dunging. By contrast, transient species were not affected by abandonment of pasturing but they are generally colonizer species (“founder effect”, Grime 1998) and very resistant to disturbance.

In this study, we showed that subordinate species are an important component of plant species diversity, which is favoured by intermediate productivity and the presence of cattle at low density (extensive management). Considering that subordinate species may have a larger influence on ecosystem processes (plant productivity, nutrient cycling, decomposition) than their relative abundance would suggest (Mariotte et al. 2013a,b), favouring these species seems to be very important for ecosystem functioning in semi-natural grasslands. Our results have direct implications for the way grasslands should be managed, when management aims at maintenance of plant biodiversity value. Indeed, while intensification and abandonment have been accelerated since the 1950s in Central Europe, findings of this study confirm the necessity to maintain intermediate levels of pasturing to preserve biodiversity and ecosystem integrity.

Acknowledgments

We acknowledge funding by the Swiss National Science Foundation (PM: project n°31003A-114139, FK: project n°3100-064116, and TS: project n°4048-064424), the NCCR Climate (AKG) and the Competence Centre in Environmental Science (CCES) of the ETH Domain through the CCES-project Mountland (AB and TS). We thank also Charlotte Vandenberghe and Aurélie Thébault for their help in this study.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX."

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Figures

Fig. 1. Relationships between site productivity (mean biomass production) and (A) the species diversity (mean species number per site), (B) the proportion of dominant species, (C) the proportion of subordinate species, and (D) the proportion of transient species for eleven semi-natural grassland sites. Curves represent significant polynomial models fitted to the relationships.

Fig. 2. Relationship between species diversity in grazed plots and (A) species diversity (mean species number per plot) in abandoned plots, (B) difference in number of dominant species, (C) difference in number of subordinates, and (D) difference in number of transients in abandoned plots compared to grazed plots for nine semi-natural grassland sites. Polynomial curves represent the significant models fitting the relationships. Straight lines indicate neutral effects of abandonment.

Mariotte, P. ; Buttler, A. ; Kohler, F. ; Gilgen, A.K. ; Spiegelberger, T. (2013) How do subordinate and dominant species in semi-natural grasslands relate to productivity and land-use change? Basic and Applied Ecology, vol. 14, n° 3; pp. 217-224

Fig.1

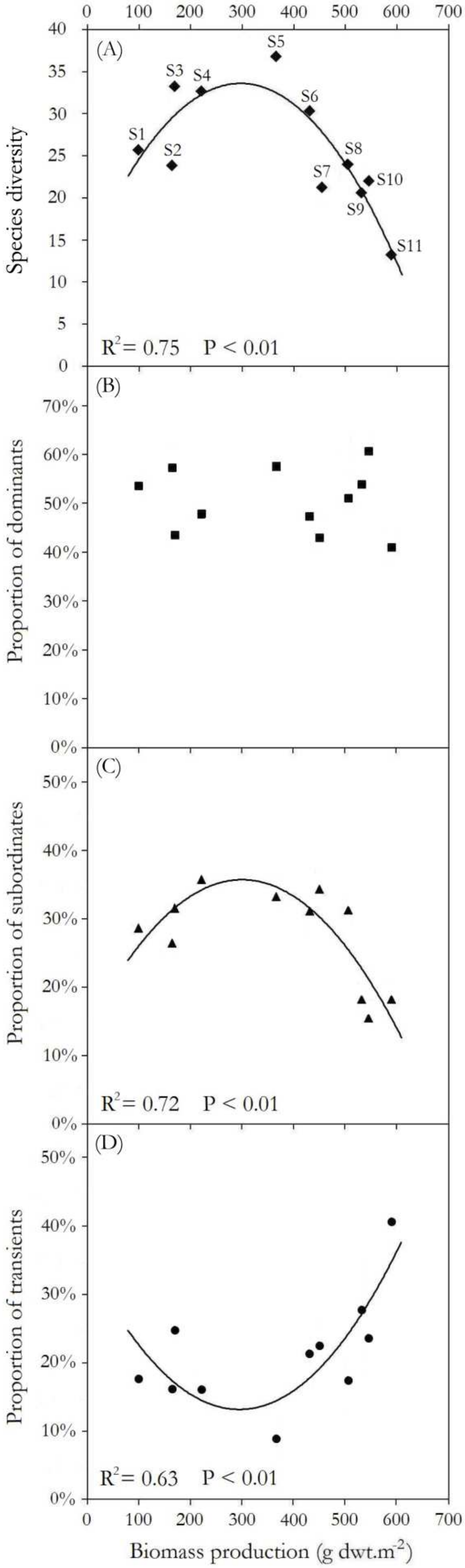
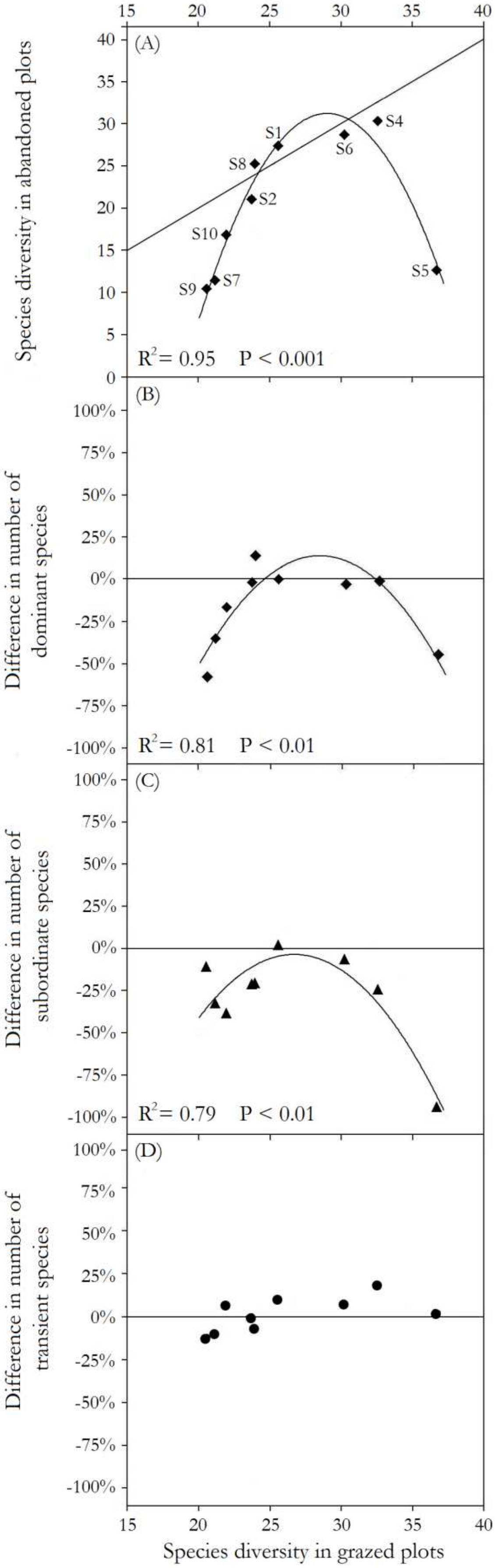


Fig. 2

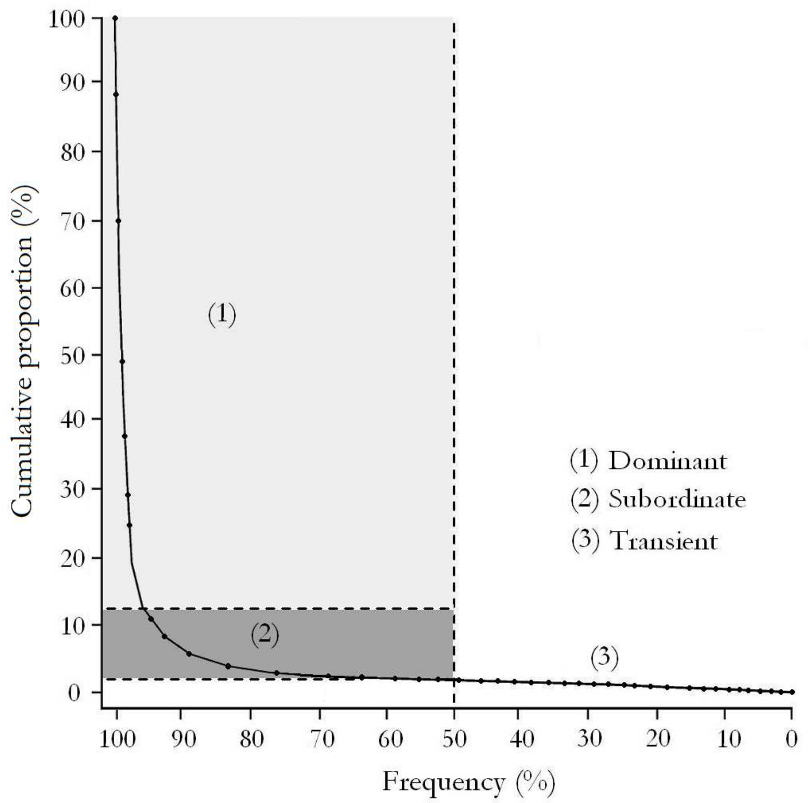

(A)
Species diversity in abandoned plots
S1
S2
S4
S5
S6
S7
S8
S9
S10
R^2= 0.95 P < 0.001
(B)
Difference in number of dominant species
R^2= 0.81 P < 0.01
(C)
Difference in number of subordinate species
R^2= 0.79 P < 0.01
(D)
Difference in number of transient species
Species diversity in grazed plots

Appendix A. Supplementary data

Appendix A: Table 1. General description of the study sites ordered by increasing productivity. In site 5, 8 and 9, the first altitude corresponds to grazed communities and the second to abandoned communities. DIN (= Dissolved inorganic nitrogen).

Code	Site	Region	Altitude (m)	Community aboveground biomass (g dwt/m2) and year of sampling	Soil fertility (DIN in µg/g dry soil)	Cattle density (per ha)	Dominant species	Analysis	Duration of abandonment (years)	References
1	Orvin	Jura, CH	1210	99 ± 7 (2002)	-	0.8	*Festuca nigrescens,Dactylis glomerata, Luzula sylvatica, Geranium sylvaticum*	A, B	3	Kohler et al. 2006a,b
2	Chablais	Alps, FR	1470	164 ± 15 (2004	12.5 ± 1.7	1	*Festuca nigrescens, Cynosurus cristatus, Deschampsia caespitosa,Taraxacum officinale*	A, B	5	Spiegelberger et al. 2006
3	La Frétaz	Jura, CH	1200	169 ± 10 (2004)	-	0.9	*Festuca nigresencs, Agrostis capillaris, Taraxacum officinale, Dactylis glomerata*	A	-	Vandenberghe et al. 2008
4	Métairie d'Evilard	Jura, CH	1210	221 ± 16 (2002)	-	0.8	*Festuca nigrescens, Agrostis capillaris, Trifolium repens, Alchemilla monticola*	A, B	3	Kohler et al. 2006ab
5	Bauges	Alps, FR	1607-1755	366 ± 14 (2004)	22.2 ± 1.6	0.8	*Festuca nigrescens, Agrostis capillaris, Anthoxanthum odoratum, Arnica montana*	A, B	5	Spiegelberger et al. 2006
6	Le Haut des Joux	Jura, CH	1240	431 ± 17 (2002)	-	0.8	*Festuca nigrescens, Agrostis capillaris, Trifolium repens, Alchemilla monticola*	A, B	3	Kohler et al. 2006a,b
7	Les Amburnex	Jura, CH	1300	455 ± 29 (2011)	-	0.8	*Festuca nigrescens, Agrostis, capillaris, Trifolium repens, Taraxacum officinale*	A, B	4	Mariotte et al. 2012a,2013a
8	Chablais	Alps, CH	1409-1517	506 ± 29 (2004)	27.3 ± 3.8	0.9	*Festuca nigrescens, Cynosurus cristatus, Poa pratensis,Taraxacum officinale*	A, B	5	Spiegelberger et al. 2006
9	Lac de Dix	Alps, CH	1507-1646	546 ± 99 (2004)	27.5 ± 2.9	0.8	*Festuca nigrescens, Cynosurus cristatus, Trifolium repens, Agrostis capillaris*	A, B	5	Spiegelberger et al. 2006
10	La Frétaz	Jura, CH	1200	532 ± 33 (2011)	-	0.9	*Festuca nigrescens, Cynosurus cristatus, Trifolium repens, Taraxacum officinale*	A, B	4	Mariotte et al.2013b
11	Früebüel	Alps, CH	980	590 ± 77 (2005)	-	-	*Festuca nigrescens, Alopecurus pratensis, Phleum pratense, Rumex acetosa*	A	-	Gilgen & Buchmann 2009

Appendix A: Figure 1. Frequency-proportion curve used for the selection of competitive hierarchical groups. Dominant and subordinate species are always present in the community and was distinguished from transient species (3), which do not persist in the vegetation, by a frequency higher than 50%. The distinction between dominant (1, grey area) and subordinate species (2, darkgrey area) is based upon cumulative proportion (%) and has been set at an arbitrary value of 12%.



Appendix A: Figure 2. Relationship between the diversity (mean species number per plot) and the productivity (mean biomass production per plot) of abandoned plots in 9 sites of semi-natural grasslands. No significant linear ($F_{1,7}$ = 0.766, P = 0.41, R^2 = 0.10) or polynomial model ($F_{2,6}$ = 0.332, P = 0.73, R^2 = 0.09) was found to link diversity and productivity.